

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 104, No. 1

MARCH 1992

PAGES 1-204

Wilson Bull., 104(1), 1992, pp. 1-21

FORAGING ECOLOGY OF SEVEN SPECIES OF NEOTROPICAL IBISES (THRESKIORNITHIDAE) DURING THE DRY SEASON IN THE LLANOS OF VENEZUELA

PETER C. FREDERICK¹ AND KEITH L. BILDSTEIN²

ABSTRACT.—We describe the relative abundance, foraging habitat, and feeding behavior of seven sympatric species of ibises (Threskiornithidae) in the Venezuelan llanos during the dry season of 1989. Scarlet (*Eudocimus ruber*), Glossy (*Plegadis falcinellus*), and Bare-faced (*Phimosus infuscatus*) ibises were the most common species. White (*E. albus*), Green (*Mesembrinibis cayennensis*), Sharp-tailed (*Cercibis oxycerca*), and Buff-necked (*Theristicus caudatus*) ibises together made up less than 8% of individuals surveyed. Multivariate analyses showed that differences in use of foraging habitat partitioned the foraging niche during the dry season, a time when little aquatic habitat is available to the birds. Foraging habitats used by the seven species were differentiated by decreasing distance to water, in the following order: Buff-necked (dry land), Sharp-tailed and Bare-faced (moist soil, occasionally in standing water), Green (water's edge), and Scarlet, White, and Glossy ibises (nearly always in standing water). Probing depth, prey size, and height of vegetation further partitioned the niche. Large differences in capture, probing, and stepping rates were found among all species. There were no differences in foraging behavior or in foraging habitat between congeneric White and Scarlet ibises. Considerable overlap in foraging habitat in space and time was seen among the three aquatic foragers (White, Scarlet, Glossy), and aggression and occasional food robbery occurred among these species. Scarlet Ibises were most aggressive and were most likely to attempt food robbery. *Received 10 Dec. 1990, accepted 26 Sept. 1991.*

Of the approximately 25 species of ibises recognized worldwide (Anonymous 1984), seven occur sympatrically in the central wetland plains, or llanos, of Venezuela. This species diversity is unmatched elsewhere in the world and is sufficient to distinguish the ciconiiform avifauna of the region from that of other Central and North American wetlands (Kushlan et al. 1985). The Scarlet Ibis (*Eudocimus ruber*), White Ibis (*Eudocimus albus*),

¹ Dept. of Wildlife and Range Sciences, 118 Newins-Ziegler Hall, Univ. of Florida, Gainesville, Florida 32611. ² Dept. of Biology, Winthrop College, Rock Hill, South Carolina 29733, and Belle W. Baruch Institute for Marine Biology and Coastal Research, Univ. of South Carolina, Columbia, South Carolina 29208.

Green Ibis (*Mesembrinibis cayennensis*), Bare-faced or Whispering Ibis (*Phimosus infuscatus*), Sharp-tailed Ibis (*Cercibis oxycerca*), Buff-necked Ibis (*Theristicus caudatus*), and Glossy Ibis (*Plegadis falcinellus*) all occur in the llanos (Gochfeld 1973, Blake 1977, Meyer de Schauensee and Phelps 1978, Thomas 1979). Although the Scarlet and White ibis, when sympatric, are known to interbreed regularly (Ramo and Busto 1987), they are not formally recognized as a single species (AOU 1983). The breeding ecology and life-histories of the Scarlet, White, Bare-faced, and Glossy ibises in the llanos are reasonably well known (French and Haverschmidt 1970, Blake 1977, Meyer de Schauensee and Phelps 1978, Luthin 1983). Little is known of the basic life histories of the other three species (Archibald et al. 1980, Luthin 1983, Ogden and Thomas 1985, Thomas and Strahl 1990). Previous work on the best-studied of the species, the Scarlet Ibis, has concentrated on breeding ecology and distribution during the wet season (French and Haverschmidt 1970; Spaans 1975, 1990; Luthin 1983; Ramo and Busto 1988; Bildstein 1990; Brouwer and van Wieringen 1990; Hislop and James 1990; van Wieringen and Brouwer 1990).

The foraging ecology of this guild is of interest for several reasons. First, the diversity of ibis species in the llanos raises questions of niche separation and behavioral foraging competition among sympatric species. Foraging niche characteristics of all seven species have been summarized qualitatively by Kushlan (1978), Ogden and Thomas (1985), and Kushlan et al. (1985). However, quantitative comparisons are lacking. Kushlan et al. (1985) suggested that similar foraging behavior and habitat use among these ibis species was likely, particularly during the dry season when receding surface water greatly reduces both potential foraging habitat and the number of prey species available. In contrast, Ogden and Thomas (1985) suggested that considerable partitioning occurred through differential use of microhabitat and probing depth during the dry season.

Second, considerable variation has been noted in the timing, numbers, and location of breeding in Scarlet, White, and Bare-faced ibises (French and Haverschmidt 1970, Kushlan 1977a, Ramo and Busto 1988, Bildstein 1990, Bildstein et al. 1990, Spaans 1990). An understanding of dry season foraging ecology may contribute to an understanding of species-specific breeding parameters and, eventually, to the conservation of these species (Archibald et al. 1980, Luthin 1983, Morales 1990, Bildstein 1990).

Here, we summarize behavioral observations and counts of mixed-species foraging flocks of ibises made at 166 locations in the central llanos of Venezuela during the dry season of 1989. Specifically, we describe relative abundances and foraging behavior of each of the species, intra- and interspecific competitive interactions, foods eaten, social interactions, foraging habitats used, and flock dynamics.

METHODS

Data were collected from 26 March 1989 to 15 April 1989 in the llanos of Venezuela, a large seasonally inundated tropical savanna (Sarmiento 1984), near the end of the dry season when surface water was confined to rivers, irrigation impoundments, natural ponds, roadside borrow pits, and oxbows. Observation sites and survey routes were located between Calabozo, San Fernando, and Bruzual in Apure state. We conducted surveys to determine species composition of foraging flocks at 166 locations along approximately 300 km of trails, roads, and highways, stopping whenever we saw ibises. Counts were made only once along each portion of the route; sizes of flocks, kinds of foraging associates, and numbers of individuals of each species were recorded during each observation. We defined foraging flocks as two or more birds foraging within 50 m of each other; singletons were birds foraging at least 50 m from other ibises. We believe our survey counts were representative of ibis populations in the llanos during the 1989 dry season because the roads we used traversed a wide variety of habitats, and because roadside ponds, ditches, and borrow pits are the last concentration points for birds during the dry season (Thomas 1979).

A number of areas along the same survey route were repeatedly sampled for (1) prey types captured and handling time of prey items (2 locations, 4 days), (2) activity as a function of time of day (96 locations, 17 days), and (3) foraging flock associates (110 locations, 11 days).

The foraging behavior of individual birds was sampled using 4-min focal observations of individuals (cf. Bildstein 1983). During each observation, a focal bird was watched through a 15–60× telescope or 10× binoculars, and its behavior recorded on a tape recorder. Recordings were transcribed within two days of each observation. The duration of each behavioral pattern was timed by stopwatch during transcription, and the number of steps, probes, gapes, lookups, captures, and aggressive interactions counted for every focal bird. Probes were typified by a forward and downward thrust of the bill into the water or substrate (Kushlan 1978, Petit and Bildstein 1987). During gapes (=head swinging, *sensu* Kushlan 1978) the bill was held slightly open and was swept with a side-to-side motion through the water in an arc pivoting about the birds' legs. Lookups were defined as an alert, nonfeeding posture with head held upright for >3 sec. Focal samples that included >30 sec of lookups ($N = 16$) were not used in our summaries of foraging rates. Captures were readily identified by a distinctive backward jerk of the head accompanied by swallowing motions. Prey size was estimated as a fraction of bill length or gape width, which, in turn, were measured on museum specimens.

For each focal sample, we recorded flock size and composition, distance to surface water, distance to and species of nearest neighbor, vegetation type and height, and foraging habitat type. Height of vegetation and depth of water were estimated in fractions of tarsometatarsal length, based on mean measurements from museum skins. Overall, we recorded the foraging behavior of 484 birds in 37 locations on 19 days of observation. Intra- and interspecific comparisons were made possible by taking focal observations of two individuals (a paired observation, *sensu* Petit and Bildstein 1987) in the same flock, either simultaneously by two different observers or within 10 min of each other by a single observer.

We used three types of multivariate analyses to determine the extent of differences among the seven species, using data from the 4-min individual observations of foraging behavior. Species was the dependent variable in all cases, with flock size, numbers of species in the flock, depth of water, height of vegetation, distance to water, time spent looking up, and numbers of steps, probes, captures, lookups, and gapes as independent variables. Because variance increased with sample size for all independent variables, data were log-transformed prior to analysis. All analyses were performed using the PC-SAS statistical analysis package (SAS Institute 1985).

Canonical variates analysis determines which linear combinations of variables best sep-

arate two or more groups. We used this method in an attempt to describe sources of variation among species and to reduce dimensionality for other analyses (James and McCulloch 1985). We also performed a multiple analysis of variance (MANOVA) to look for specific differences among the centroids of species along multivariate axes. Finally, we used discriminant function analysis to evaluate the use of the habitat and behavioral variables in distinguishing among species through reclassification.

RESULTS

Species composition.—Scarlet, Glossy, and Bare-faced ibises (in that order) were by far the most common species of ibises seen in surveys (92% of all individuals, Table 1). The other four species made up a total of less than 8% of the ibises seen. Juveniles and sub-adults made up 13% of the Scarlet Ibises seen (Table 1); small sample sizes and lack of a distinctive juvenal plumage precluded the determination of age composition in the other species.

Size of foraging flocks and numbers of foraging associates.—Buff-necked and Sharp-tailed ibises were usually found in small, conspecific flocks, often well away from other species (Table 2). Flocks of Buff-necked Ibises usually comprised 2–6 individuals, with courtship activities seen in more than half of the flocks. We found three active nests of this species in the vicinity of Hato El Frio near Mantecal between 11 and 14 April, suggesting that at least small numbers of Buff-necked Ibises breed late in the dry season (Ogden and Thomas 1985). Buff-necked Ibises were more likely to be found in single-species flocks and as singletons than other species, and this species had the greatest mean nearest-neighbor distance (Table 3).

Despite a tendency for Sharp-tailed Ibises to feed in small single-species flocks with large nearest-neighbor distances, individuals of this species rarely foraged as singletons (2.9% of flocks, the lowest of any species). Forty-two percent of the Sharp-tailed Ibis flocks we saw ($N = 24$) were composed of two adults, often of discernibly different body sizes and facial coloration, suggesting the individuals were male-female pairs (Blake 1977). Twenty-five percent of Sharp-tailed Ibis flocks also included a third, notably smaller individual, with relatively drab and undeveloped facial coloration, possibly a juvenile (Luthin 1983). We observed frequent calling among presumptive pair and family members, as well as gentle bill-pecking of the larger birds by smaller individuals, sometimes followed by allopreening of smaller birds by the larger individuals.

Glossy, Bare-faced, and Scarlet ibises were consistently seen in larger flocks than were the other species. All three species were frequently found with other species of ibises (Table 2) as well as with domestic animals (Table 3), and White, Glossy and Scarlet ibises were often found feeding near other species of waterbirds (Table 3). Bare-faced Ibises, which often associated with other species of ibises and domestic animals, almost never

TABLE 1
 NUMBERS OF IBISES SEEN ON SURVEYS DURING THE DRY SEASON IN THE VENEZUELAN LLANOS (NUMBERS EXPRESSED IN PARENTHESES ARE PERCENTAGES OF TOTAL BIRDS SEEN ON SURVEY)

Survey route	Species ^a										Total
	SCIB		WHIB	GLIB	GRIB	BFIB	BNIB	STIB	Total		
	Adults	Juveniles							Adults	Juveniles	
Calabozo to San Fernando ^b	84 (30)	31 (11)	2 (07)	4 (1)	56 (20)	84 (30)	17 (6)	5 (2)	283		
San Fernando to Bruzual	299 (30)	25 (3)	15 (1)	474 (47)	0 (0)	187 (18)	10 (1)	2 (0.2)	1012		
Entire route	383 (30)	56 (4)	17 (1)	478 (37)	56 (4)	271 (21)	27 (2)	7 (1)	1295 (100)		

^a SCIB = Scarlet Ibis, WHIB = White Ibis, GLIB = Glossy Ibis, GRIB = Green Ibis, BFIB = Buff-necked Ibis, BNIB = Bald-faced Ibis, STIB = Sharp-tailed Ibis.
^b The survey route is divided to reflect potential differences in species composition from differences in habitat between the central (Calabozo-San Fernando) and western (San Fernando-Bruzual) sections of the llanos.

TABLE 2
SUMMARY OF THE FLOCKING BEHAVIOR OF SEVEN SPECIES OF IBISES DURING 4-MIN FOCAL OBSERVATIONS IN THE DRY SEASON IN THE VENEZUELAN LLANOS

Species	No. flocks	Mean no. ibises in flock (sd) ^b	Mean no. con- specifics in flock (sd)	Percent of flocks of focal species containing ^a							Single bird
				SCIB	WHIB	GLIB	GRIB	BFIB	Con- specifics only		
SCIB	271	17.64 (45.82)	15.30 (45.04)	100	11	36	26	26	35	13	
WHIB	55	4.10 (1.99)	1.76 (1.68)	91	100	58	27	36	6	6	
GLIB	132	26.17 (62.87)	12.34 (41.19)	76	24	100	33	28	59	16	
GRIB	143	9.13 (11.54)	2.73 (2.60)	50	11	30	100	30	29	13	
BFIB	161	15.48 (47.45)	3.67 (6.18)	44	12	23	27	100	39	19	
BNIB	24	6.83 (8.74)	2.54 (1.78)	21	8	13	21	21	71	21	
STIB	31	5.58 (7.82)	1.97 (0.07)	13	3	10	26	19	52	3	

^a Compiled from flock censuses and ad lib behavioral samples of flocks.

^b Total numbers of individuals of all ibis species in flock. Does not include numbers of other waterbirds present and does not count the focal individual.

TABLE 3

SUMMARY OF NEAREST-NEIGHBOR ASSOCIATIONS IN FEEDING FLOCKS OF SEVEN SPECIES OF NEOTROPICAL IBISES, SHOWING NEAREST-NEIGHBOR ASSOCIATIONS AND MEAN NEAREST-NEIGHBOR DISTANCES

	Focal species						
	SCIB (N = 50)	WHIB (N = 12)	GLIB (N = 14)	GRIB (N = 36)	BFIB (N = 20)	BNIB (N = 44)	STIB (N = 19)
Nearest neighbor species							
SCIB	72 ^a	92	43	8	8	2	0
WHIB	1	0	0	0	0	0	0
GLIB	8	0	57	0	3	0	5
GRIB	0	0	0	9	0	2	5
BFIB	6	8	0	0	83	5	21
BNIB	0	0	0	0	0	91	0
STIB	2	0	0	0	6	0	68
Nearest neighbor							
Distance (m)							
Mean	2.4	2.4	1.4	4.2	3.4	8.2	6.6
SD	3.79	1.97	0.64	4.97	2.95	8.88	8.25
N	45	11	11	19	32	35	17
Flocking Associates (% of flocks)							
Domestic animals ^b	16	17	4	8	18	3	3
Other waterbirds ^c	43	33	73	18	0	16	21

^a Percent of total nearest-neighbor observations for focal species.

^b Primarily cattle and horses, occasionally swine or burros.

^c Primarily White-faced Whistling-Ducks (*Dendrocygna viduata*), Black-bellied Whistling-Ducks (*D. autumnalis*), Great Egrets (*Casmerodius albus*), Snowy Egrets (*Egretta thula*), Rufescent Tiger-Herons (*Tigrisoma lineatum*), Wood Storks (*Mycteria americana*), Jabiru Storks (*Jabiru mycteria*), Cattle Egrets (*Bubulcus ibis*), and Roseate Spoonbills (*Ajaia ajaja*), with occasional Crested Caracaras (*Polyborus plancus*), Horned Screamers (*Anhima cornuta*), Comb Ducks (*Sarkidiornis melanotos*), and Black-necked Stilts (*Himantopus himantopus*).

foraged with non-ibis waterbirds. Glossy, Scarlet, and Bare-faced ibises maintained the smallest nearest-neighbor distances within foraging flocks, with Glossy Ibises occurring most often in conspecific-only flocks, and tolerating the most dense packing. Although White Ibises were almost always associated with Scarlet Ibises (91% of flocks, 92% of nearest neighbors), this species tended to be found in flocks containing fewer birds, and fewer species of ibises than were Scarlet Ibises. Green Ibises usually fed in a dispersed fashion on the periphery of mixed-species flocks, usually with other Green Ibises as their nearest neighbor.

Time of day and feeding activity.—Scarlet and Glossy ibises were more active during the early morning hours than later in the day (Fig. 1), a trend which was not as pronounced in Green Ibises. Bare-faced Ibises showed a peak in activity during mid-day. Although sample sizes were

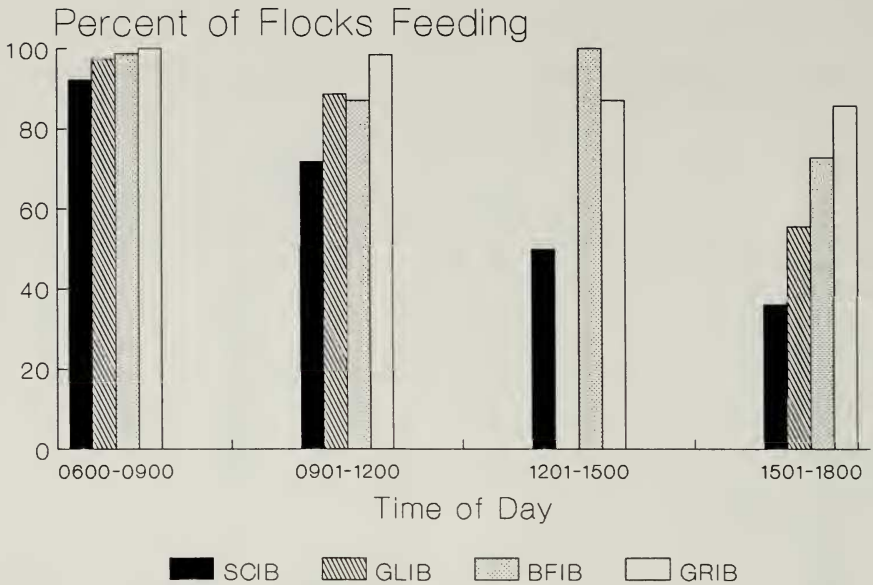


FIG. 1. Feeding behavior of Scarlet, Glossy, Bare-faced, and Green ibises as a function of time of day.

small, Sharp-tailed Ibises also appeared to be most active during the morning, while Buff-necked Ibises seemed to be active at all hours of the day. We did not search for ibises after sundown, and the possibility exists that some species forage at night as well.

Foraging habitat.—All of the sites at which we watched ibises were relatively open, with trees generally spaced at least 100 m apart. Although we checked other habitats on a number of occasions, we never saw ibises foraging in gallery or riverine forest habitats as has been reported for Green and Sharp-tailed ibises during the wet season (Wood 1923, Luthin 1983). Buff-necked Ibises almost always foraged in parched, dusty fields and recently burned areas in relatively short stubble or other low vegetation. Even so, Buff-necked Ibises foraged within 200 m of water. The

→

FIG. 2. Summary of habitat types in which foraging ibises were observed during 4-min focal samples. Esteros are oxbows of permanent or temporary river containing pools of standing water and green vegetation. Ponds were naturally occurring roadside ponds or depressions at least 5 cm deep. Borrow pits were roadside ditches from which large amounts of material had been taken for roadbuilding.

Percent of Observations

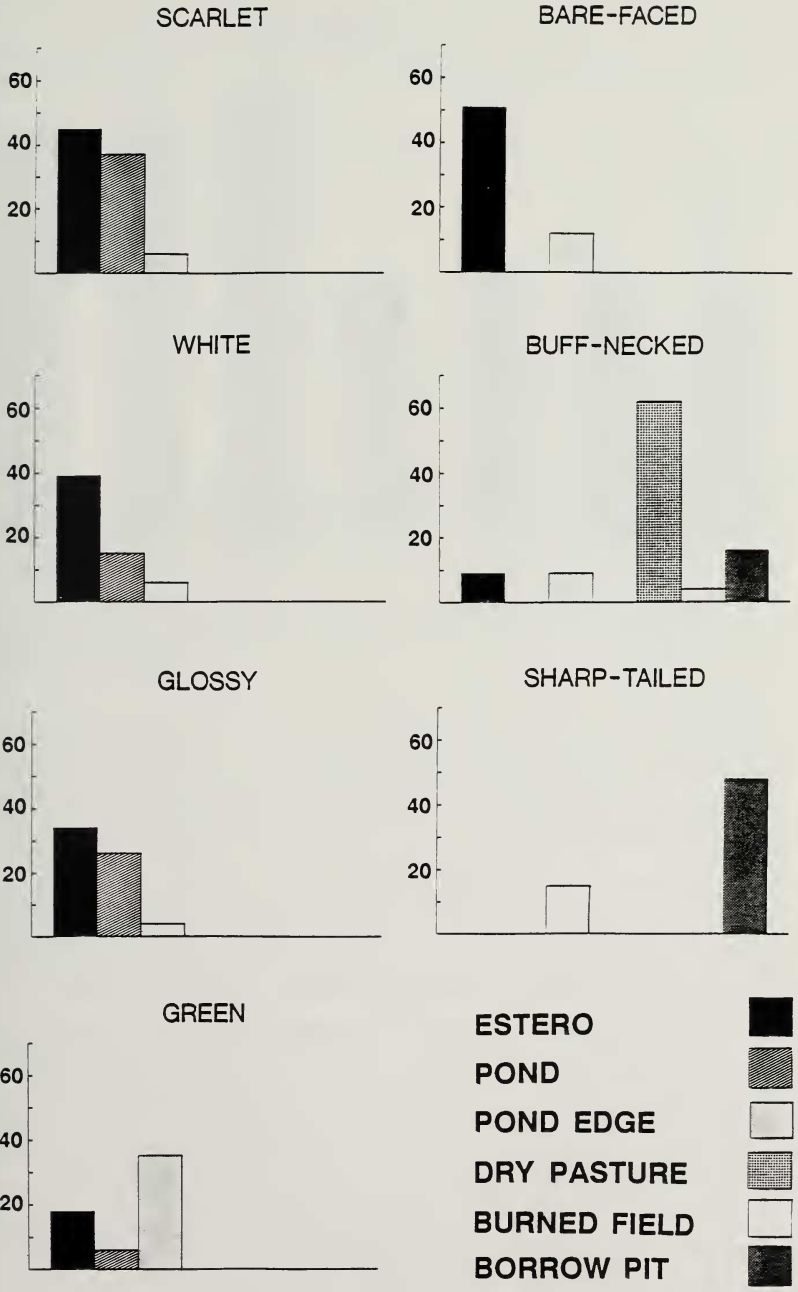


TABLE 4
SUMMARY OF FORAGING HABITAT CHARACTERISTICS OF FOCAL INDIVIDUALS^a

Species	N	Percent of individuals in water	Distance to water (m)	Water depth (cm)	Vegetation height (cm)
SCIB	153	93	3.4 ± 12.7	4.6 ± 3.5	17.5 ± 11.0
WHIB	33	78	10.0 ± 24.1	3.1 ± 2.8	19.6 ± 9.5
GLIB	55	94	0.2 ± 1.0	4.2 ± 2.7	12.8 ± 7.6
GRIB	55	94	11.4 ± 22.1	1.0 ± 1.4	11.4 ± 5.5
BFIB	67	17	63.2 ± 81.8	0.8 ± 1.9	12.5 ± 8.4
BNIB	71	2	122.9 ± 95.8	0.1 ± 0.3	8.3 ± 5.3
STIB	50	46	47.4 ± 78.9	1.6 ± 2.2	6.3 ± 7.7

^a All values are means ± one SD.

other six species of ibises were more closely associated with moist soil and standing water. Esteros (moist to shallowly flooded oxbow meadows) were commonly used by all species, except Buff-necked and Sharp-tailed ibises. Both Sharp-tailed and Green ibises used the moist edges of pools, ponds, and wetlands, although both species were rarely found feeding in water deeper than 2 cm (Fig. 2, Table 4). Although Green and Bare-faced ibises fed at similar sites, Bare-faced ibises foraged in somewhat taller vegetation than did Green Ibises and were rarely found foraging in water. We noticed an increase in relative numbers of Sharp-tailed Ibises in the flatter and more open south-western llanos, where they often fed in borrow pits that were usually devoid of emergent vegetation. This species seemed to prefer shorter vegetation than did either Green or Bare-faced ibises (Table 4).

Scarlet, White, and Glossy ibises foraged in similar habitats overall (Fig. 2). They often foraged in relatively deep water, and when foraging on dry ground were very close to open water. Scarlet and White ibises were found in somewhat taller vegetation than other species of ibises, although the differences in mean vegetation height were not large among the three aquatic species (Table 4). These three species were distinct from the others in having relatively long legs for their body size (Fig. 3).

Foraging behavior.—Buff-necked Ibises had by far the highest stepping, and lowest probing rates of any species (Table 5). Probing behavior in this species consisted of shallow probes and pecks directed at the surface of the hard, dry substrate. Sharp-tailed Ibises had the second highest stepping rates, the lowest probing efficiencies (captures/probe), low capture rates, and probed more rapidly and deeply than any other species. As a result, then, their bills were often covered with mud to the gape, a

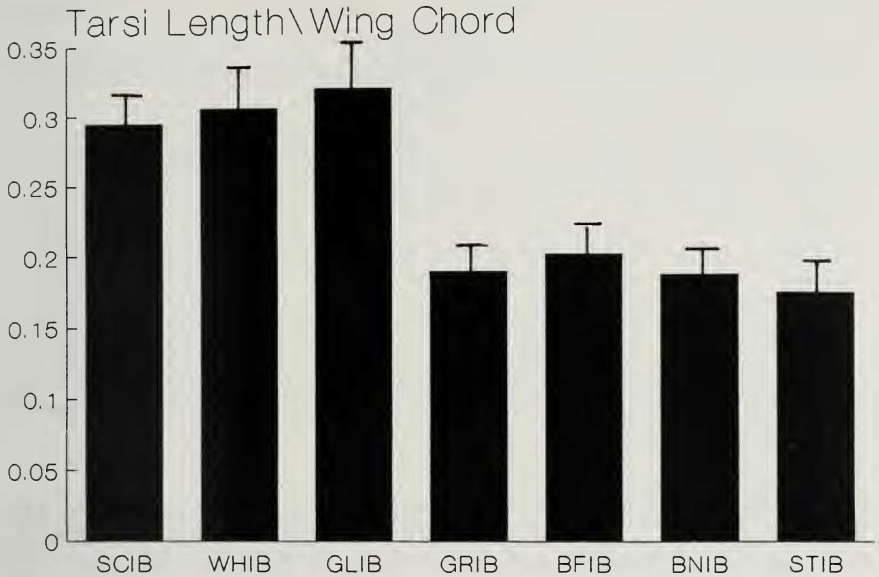


FIG. 3. Mean ratios of the length of tarsometatarsus to wing chord in seven species of ibises. Measurements are from museum specimens collected in the llanos. Vertical lines are + one standard deviation.

phenomenon seen rarely in only one other species, the Green Ibis. Green Ibises showed high capture rates and probing efficiencies, coupled with intermediate rates of stepping and probing. Glossy Ibises had the highest capture rates of any of the species, as well as very high probing rates and probing efficiencies. Glossy Ibises exhibited relatively slow stepping rates because they intensively probed the small area around their bodies. Bare-faced, White, and Scarlet ibises had nearly identical capture and probing rates, although Scarlet Ibises stepped less often than Bare-faced or White ibises.

Comparisons of the foraging behavior of paired White and Scarlet ibises feeding in the same flocks ($N = 17$ pairs) showed no significant differences (Wilcoxon Matched-Pairs Signed Ranks tests, $P > 0.05$) except for probing efficiency, in which White Ibises were more efficient than were Scarlet Ibises ($P = 0.04$). No significant differences were found in the foraging behavior of paired Glossy and Scarlet ibises ($N = 13$ pairs).

Multivariate analyses.—All six potential composite variables constructed by the canonical correlates analysis were highly significant ($P < 0.0001$), and no reduction in dimensionality was possible using this analysis. The first three canonical correlates accounted for over 97% of the total vari-

TABLE 5
SUMMARY OF THE MEAN FORAGING RATES OF FOCAL INDIVIDUALS OF SEVEN SPECIES OF
IBISES

Species	Steps/ min.	Probes/ min.	Probes/ step	Cap- tures/ min.	Cap- tures/ probe	Cap- tures/ step	Look- ups/ min.	N ^a
SCIB	16.2	34.6	2.2	1.5	0.04	0.10	1.20	124 (10)
WHIB	24.4	34.2	1.4	1.4	0.04	0.06	0.89	30 (7)
GLIB	12.5	41.5	3.3	3.3	0.08	0.27	0.81	48 (5)
GRIB	17.6	30.0	1.7	1.9	0.06	1.06	0.89	58 (9)
BFIB	23.1	35.0	1.5	1.4	0.04	0.06	0.81	60 (10)
BNIB	62.5	26.4	0.4	0.5	0.02	0.007	0.24	32 (17)
STIB	26.7	44.8	1.7	0.7	0.01	0.24	0.54	41 (11)

^a Numbers of individuals (numbers of sites).

ation in the model and were weighted heavily by habitat variables, and relatively little by behavioral variables. Scatter plots of the seven species along these three axes did not result in distinct separations of species, and are not presented. The overall MANOVA model showed a significant effect of species ($P < 0.0001$), as did all 21 pairwise combinations of species ($P < 0.0001$), indicating that the centroids of each species separate distinctly along the multivariate axes. Each of the habitat and behavioral variables also showed significant effects, with the exception of gaping ($P = 0.226$).

Discriminant function analysis revealed relatively low reclassification ability to species, using the behavioral and habitat variables (Table 6). While the discriminatory abilities of the model were significantly different

TABLE 6
PERCENT OF OBSERVATIONS OF EACH SPECIES RECLASSIFIED CORRECTLY TO SPECIES BY THE
DISCRIMINANT FUNCTION ANALYSIS

Species	Percent classified correctly
SCIB	66.6
WHIB	84.4
GLIB	61.2
GRIB	54.5
BFIB	50.0
BNIB	75.0
STIB	51.2
Total percent correct	63.3

TABLE 7

SUMMARY OF SIZES OF PREY EATEN BY SEVEN SPECIES OF NEOTROPICAL IBISES DURING THE DRY SEASON^a

	SCIB	WHIB	GLIB	GRIB	BFIB	BNIB	STIB
Total captures	866	166	91	482	329	63	103
Percent							
<1 cm ^b	87	93	91	98	98	85	90
>1 cm	11	8	9	1	2	13	10
1–2 cm	4	2	8	1	0	3	3
2–3 cm	1	<1	0	0	<1	0	<1
>3 cm	6	5	1	<1	1	10	6

^a Compiled both from four-minute focal animal samples and ad lib surveys of flocks.

from a random reclassification scheme ($\chi^2 = 668$, $df = 6$, $P \ll 0.0001$), only 63% of all observations were classified correctly, and in only White and Buff-necked ibises did the reclassification efficiency exceed 75%.

Prey characteristics.—In most cases, we were unable to identify prey because most items were very small (<1 cm), and were swallowed within 2 sec of capture (Table 7). From their shape, size, and the manner in which they were handled, we believe most small prey items were arthropods, along with small numbers of annelid worms and (in the case of Green and Glossy ibises), small gastropods.

Buff-necked and Scarlet ibises included a greater proportion of large prey in their diets than did the other species (14 and 11% of captures over 1 cm, respectively), while almost all of the diet of Green and Bare-faced ibises consisted of prey <1 cm (Table 7). The most commonly identified large items were hemipteran water beetles (Belostomatidae, Naucoridae, Corixidae) and aquatic beetles (Gyrinidae). Giant water bugs, (3–10 cm) accounted for 90% of Scarlet Ibis captures over 1 cm in length. Because of their large size and escape tactics, giant waterbugs were associated with long handling times and frequent piracy attempts.

Aggressive interactions and prey robbery.—Aggressive interactions were rare among foraging Buff-necked or Sharp-tailed ibises, perhaps because both species tended to feed in dispersed, single-species flocks and family groups (Table 8). Similarly, Green Ibises rarely engaged in aggressive interactions, probably because they rarely came into contact with other species.

Scarlet, White, Bare-faced, and Glossy ibises all were regularly involved in aggressive encounters. Scarlet Ibises engaged in aggression most fre-

TABLE 8
SUMMARY OF AGGRESSIVE TENDENCIES OF SEVEN SPECIES OF IBISES IN FORAGING FLOCKS

Species	Minutes observed ^a	Attacks performed ^b /min	Attacks received/min	Aggression ratio ^c
SCIB:				
Males	460	8.8 ¹	2.9 ^{1,2}	3.09
Females	70	7.7 ^{1,2}	6.0 ¹	1.00
Both sexes	538	8.7 ¹	3.4 ¹	2.52
WHIB:				
Males	60	7.0 ¹	1.0 ^{1,2}	7.00
Females	52	0.0 ²	8.1 ²	0.00
Both sexes	122	4.4 ²	6.4 ¹	0.69
GLIB	194	1.2 ³	3.1 ^{1,3}	0.40
GRIB	246	0.5 ^{2,4}	1.0 ²	0.50
BFIB	237	1.8 ^{2,3}	1.5 ^{2,3}	1.17
BNIB	219	0.0 ³	0.5 ²	0.00
STIB	171	0.4 ³	0.0 ²	0.00

^a Minutes of observation of focal birds in flocks only.

^b Column entries with different superscript numbers differ significantly from one another ($P < 0.05$, χ^2 goodness of fit test, 1 df with Yates correction).

^c Attacks performed/attacks received.

quently and initiated aggressive interactions at higher rates, and in higher proportion than did the other species. Glossy Ibises were particularly unaggressive towards conspecifics, even though this species foraged in tight conspecific groups. On one occasion, we observed a Glossy Ibis foraging for over 30 sec with its neck extended over that of its nearest neighbor.

Despite their close association with Scarlet Ibises, White Ibises initiated aggressive interactions only half as often as did Scarlet Ibises ($P = 0.073$, χ^2 goodness of fit test), and were recipients of aggression twice as often as were Scarlet Ibises ($P = 0.0048$). The species difference is largely the result of the behavior of female White Ibises. Although male Scarlet Ibises, female Scarlet Ibises, and male White Ibises did not differ in rates of aggression, all initiated aggression at significantly higher rates than did female White Ibises (Table 8). Female White Ibises also were recipients of aggression significantly more often than were female Scarlet Ibises.

While Scarlet Ibises were more likely to attack other species, these did not always result in displacement (Table 9). Glossy Ibises attacked and displaced Scarlet Ibises in 18% of their aggressive interactions, and White Ibises displaced Scarlet Ibises in 45% of their aggressive interactions.

TABLE 9
NUMBERS OF AGGRESSIVE INTERACTIONS AMONG SEVEN SPECIES OF IBISES IN FORAGING
FLOCKS THAT DID NOT INVOLVE PREY

Recipient	Aggressor					
	SCIB	WHIB	GLIB	GRIB	BFIB	Other ^a
SCIB	52	10	0	3	0	2
WHIB	12	2	0	0	0	0
GLIB	13	0	0	0	1	0
GRIB	5	0	0	0	0	0
BFIB	2	0	0	0	12	0
Other ^b	4	0	0	2	0	0

^a Includes White-faced Whistling-Duck and Wattled Jacana (*Jacana jacana*).

^b Includes STIB, Southern Lapwings (*Vanellus chilensis*), White-faced Whistling-Ducks, and Great Egrets.

Scarlet Ibises were socially dominant to Green and Bare-faced ibises. Among species, rates of aggression were negatively correlated with mean nearest neighbor distances ($R_s = 0.75, 0.86, P < 0.005$ for initiating and receiving aggression, respectively) (Tables 3 and 8).

Of a total of 158 aggressive intra- and interspecific interactions, 33% occurred when the recipient of aggression had food in its bill or was actively pursuing prey. In 18 of these cases (11% of the total), the aggressor clearly attempted to snatch prey from the recipient. Attempts at food robbery were successful in at least three cases (a minimum success rate of 13%). Scarlet Ibises were the most likely species to attempt food robbery (67% of all attempts), with White (17%) and Glossy (16.6%) ibises being the only other two species to attempt food robbery. All attempts at piracy by Scarlet and White ibises were made by males, and only Scarlet Ibises were successful. Scarlet Ibises were victims of attempted piracy 15 times (83% of the total, 2 females, 10 males), Glossy Ibises twice (11%), and Bare-faced Ibises once (6%).

Food robbery was used by some male Scarlet Ibises more than others. Four individuals at one site attempted to steal giant water bugs on a total of five occasions from Glossy Ibises foraging in groups, and apparently also captured several beetles as a result of the beater effect of the flock. Each of the four Scarlet Ibises also repeatedly chased conspecifics from the flock of Glossy Ibises, suggesting that the pirating ibises were defending the flocks as a resource.

We also observed four Crested Caracaras (*Polyborus plancus*) and one Savanna Hawk (*Heterospizias meridionalis*) closely following mixed-spe-

cies ibis foraging groups, attempting to steal giant water beetles from Scarlet and Glossy ibises. Only one of these attempts was successful, directed at a Scarlet Ibis which had in turn stolen the beetle from a Glossy Ibis.

Other foraging techniques. — Foraging flocks of Scarlet, White, and Bare-faced ibises were over twice as likely as those involving other ibis species to include domestic animals (Table 3), and on several occasions, we noted groups of Scarlet, White and Bare-faced ibises closely (<3 m) following domestic cows and horses, apparently capturing insects disturbed by the animal's footsteps. We also observed Scarlet Ibises closely following flocks of 3–50 White-faced Whistling-Ducks (*Dendrocygna viduata*) on 10 occasions, apparently feeding on aquatic insects disturbed by the ducks. The ibises occasionally pecked at the closest ducks, which appeared to keep the flock moving. Groups of 2–16 White-faced Whistling-Ducks similarly foraged behind individual Scarlet Ibises on four occasions, repeatedly displacing one another to gain a spot immediately behind the ibis.

On six occasions, we noted single Bare-faced Ibises foraging alternately in two areas of less than 1 m² each, 2–6 m apart in medium to tall grass on moist ground. Individuals probed intensively in one of the areas for 1–6 min, then walked rapidly to the other site and began probing. Three to five trips between the two sites occurred during each observation. We were unable to identify prey items extracted from these intensively worked sites.

DISCUSSION

Species composition. — The relative abundances of the seven ibis species we report differ little from those found by Kushlan et al. (1985), Aguillera (unpubl. data), and Ogden and Thomas (1985). In all three of the previous studies, Scarlet Ibises were the most abundant, with White, Buff-necked and Sharp-tailed ibises making up a very small percentage of the ibis community. Green Ibises comprised less than five percent of the ibises seen by Aguillera (unpubl. data) and ourselves, and Ogden and Thomas (1985) describe them as common in pairs or small groups. In contrast, Kushlan et al. (1985) reported that Green Ibises represented over 36% of the ibises they observed. This considerable departure from the other studies suggests that the species concentrates in certain areas during the dry season, that Green Ibises leave portions of the area entirely during the dry season, or that other species decrease in proportion seasonally. There is also considerable variation in relative abundances of Glossy Ibises among studies, suggesting a slow increase in the abundance of this species since Gochfeld's first report of abundance (Gochfeld 1973, Kushlan et al. 1985, Aguillera unpubl. data from 1981–1982, this study).

Foraging niche relationships. — Our descriptions of foraging habitat and

behavior confirm earlier reports by Luthin (1983), Kushlan et al. (1985), French and Haverschmidt (1970), Ogden and Thomas (1985), and Brouwer and van Wieringen (1990), and support the idea that these seven species of ibises coexist with considerable partitioning of the foraging resource even during the dry season (Ogden and Thomas 1985). Our multivariate analyses suggest (1) that variation in habitat and behavior is sufficient to separate any species-pair along multivariate axes, (2) overlap in the centroids of species on these axes is too extensive to permit an accurate reclassification using the variables we recorded, and (3) taken together, none of the habitat and behavioral variables we used can be excluded as a significant source of variation among species.

The most obvious mechanism partitioning the feeding niches of ibises during the dry season appears to be habitat. Buff-necked Ibises were the only ibis species that regularly foraged on dry land. This species was rarely seen feeding in standing water, even in the absence of other species. Sharp-tailed Ibises also were distinctive in their use of habitat, almost never being found in esteros or broad areas of open water. Two species-assemblages could be further distinguished along an aquatic-terrestrial gradient. Sharp-tailed, Green, and Bare-faced ibises were often found foraging in moist soil as well as along the edge of standing water. Although each of these three species was occasionally found foraging in water, they did so only when other ibis species were absent, suggesting behavioral avoidance. White, Scarlet, and Glossy ibises were the three species with the largest legs in proportion to wing length, were rarely found out of water, and usually foraged in depths of at least 3 cm. Thus on the basis of habitat alone, the potential for direct competition for food seems limited to the Sharp-tailed-Green-Bare-faced group, and the Scarlet-White-Glossy group.

The three species that foraged in moist, but rarely inundated, areas differed in their use of microhabitats. Bare-faced Ibises were rarely (17%) found foraging in standing surface water, and appeared to be restricted to moist areas. Green Ibises were a water's-edge specialist, being found in shallow water 94% of the time, and nearly always within two meters of the shoreline. Sharp-tailed Ibises fed in moist soil and at the water's edge. Their preference for areas with little or no vegetation may be important in limiting contact with Bare-faced and Green ibises. We suspect that the potential for niche overlap with Green Ibises in water's-edge habitat also is reduced by a noticeable difference in probing depths (first suggested by Ogden and Thomas [1985]), that probably results in the higher proportion of large prey consumed by the deeper-probing Sharp-tailed Ibises. Behavioral avoidance also appears to be an important mechanism for reducing dry-season foraging overlap among the three moist-ground species. Green, Sharp-tailed, and Bare-faced ibises had relatively

high probabilities of foraging in single-species flocks, and all showed large nearest-neighbor distances while feeding.

The three aquatic feeders (White, Scarlet, and Glossy ibises) exhibited fewer differences in foraging habitat use. All three foraged in essentially the same habitats (deep, open water), and all used the same foraging techniques (probing rapidly into the surface layer of substrate). Foraging niche overlap between White and Scarlet ibises, and Glossy Ibises may be a relatively recent phenomenon, if, as Gochfeld (1973) suggests, Glossy Ibises have only become abundant in the llanos during this century. Aggressive behavioral interactions among these three aquatic species were certainly the most noticeable of any species combination, the majority of which (>60%) did not involve disputes over captured or pursued prey. Tendencies to interact aggressively were inversely related to nearest-neighbor distances, possibly as a result of the tremendous reduction in available foraging habitat during the dry season.

Despite incomplete dominance, Scarlet Ibises were clearly more aggressive than Glossy Ibises within the same habitat. The increased aggressive tendency of Scarlet Ibises during feeding appears to be a sexually selected feature of the genus (Rudegeair 1975, Kushlan and Kushlan 1975, Ramo and Busto 1985, Frederick 1987), but may also be of selective advantage during feeding. While we were unable to measure the extent to which Scarlet Ibises might have benefited from food robbery, we suggest that their aggressiveness provides them with access to large prey, both directly via prey robbery and indirectly via defense of groups of hetero-specific beaters.

Although Glossy, White, and Scarlet ibises may compete for small, predominantly arthropod prey, Glossy Ibises took fewer large prey than did Scarlet Ibises or White Ibises.

White and Scarlet ibises showed little separation in habitat use, foraging behavior, or size and type of prey eaten. White Ibises foraged in slightly shallower water, more often on dry ground, farther from open water and were generally in smaller flocks than Scarlet Ibises. Despite these differences, White Ibises almost always fed with Scarlet Ibises (over 90% of flocks). Similarly, 92% of nearest neighbors of White Ibises were Scarlet Ibises, and White Ibises were never observed with another White Ibis as their nearest neighbor. Considerable aggression occurs between those two species during foraging, and neither species dominates. While Scarlet Ibises seemed to be more aggressive as a whole, this difference is largely the result of smaller female White Ibises (cf. Kushlan 1977b) being less aggressive than Scarlet Ibises of either sex. Overall, our observations do not suggest that substantial differences exist in the foraging ecology of the two species, supporting the idea that Scarlet and White Ibises in the llanos are races of the same species (Ramo and Busto 1987).

Both Kushlan et al. (1985) and van Wieringen and Brouwer (1990) reported that during the wet season Scarlet Ibises in the llanos often foraged on moist ground that was not inundated by standing water. We almost never saw Scarlet Ibises foraging out of water, suggesting that the dynamics of soil-dwelling prey may limit dry-season foraging to inundated areas. If true, the niche of Scarlet Ibises may be considerably reduced during the dry season. Similarly, the inundated gallery-forest described as foraging habitat for Green and Sharp-tailed ibises during the wet season (Luthin 1983) and those reported here indicate these species also shift foraging habitat with season.

Our observations confirm that the majority of foods eaten during the dry season by all seven species are insects, together with small numbers of anurans, crustaceans, gastropods, and oligochaetes (Ogden and Thomas 1985, Kushlan et al. 1985, Luthin 1983, and Brouwer and van Wieringen 1990). Despite the locally high densities of fishes during the dry season (pers. obs., Kushlan et al. 1985, Morales and Pacheco 1986), we never saw ibises consume fishes, even though the three aquatic species we watched often foraged together with piscivorous storks, herons, egrets, and tiger-herons.

Our observations of courtship and nesting of Buff-necked Ibises in the southwestern llanos confirm that at least one peak of nesting in this species occurs near the end of the dry season (Ogden and Thomas 1985, Aguillera, unpubl. data). This is particularly intriguing, in light of the fact that this species had the lowest rate of captures of any species (0.49/min). It is possible that more productive foraging by this species occurs in habitats (such as burning fields) which were not sampled during our surveys.

Finally, we caution that as our observations were made during a single dry season, our results may not be representative of foraging behavior and habitat use in the wet season (above) or in other years.

ACKNOWLEDGMENTS

We thank J. Ayarzagüena, B. Busto, C. Luthin, F. Espinoza, C. Ramo, G. Rios, J. Robinson, and the staff of the Estacion Biologica El Frio for help in planning and executing our field work. We especially thank T. Blohm, C. Coronel, and the C. A. Invega company for allowing us access to their land and for accommodations in the field. C. Marrero assisted us in identifying aquatic insects, and J. Smallwood, S. Linda, and R. O'Brien provided statistical guidance. B. Trent-Thomas, C. Blem, and an anonymous reviewer made numerous helpful suggestions on an earlier draft of this paper. This work was supported in part by the Whitehall Foundation, the American Philosophical Society, the NSF-LTER Program and by a sabbatical leave from Winthrop College, to KLB. This is contribution number 883 of the Belle Baruch Institute of Marine Biology and Coastal Research.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds, 6th edition. A.O.U., Washington, D.C.

- ANONYMOUS. 1984. World working group on storks, ibises and spoonbills, Rept. 2:1984. ICBP, Walsrode, West Germany.
- ARCHIBALD, G., S. LANTIS, L. LANTIS, AND I. MUNETCHIKA. 1980. Endangered ibises (Threskiornithidae): their future in the wild and captivity. *Inter. Zoo Yearb.* 20:6-17.
- BILDSTEIN, K. L. 1983. Age-related differences in the flocking and foraging behavior of White Ibises in a South Carolina salt marsh. *Col. Waterbirds* 7:146-148.
- . 1990. Status, conservation and management of the Scarlet Ibis (*Eudocimus ruber*) in the Caroni Swamp, Trinidad, West Indies. *Biol. Conserv.* 54:61-78.
- , W. POST, J. JOHNSTON, AND P. C. FREDERICK. 1990. Freshwater wetlands, rainfall, and the breeding ecology of White Ibises in coastal South Carolina. *Wilson Bull.* 102:84-98.
- BLAKE, E. 1977. *Manual of Neotropical birds. Vol. 1.* Univ. of Chicago Press, Chicago, Illinois.
- BROUWER, K. AND M. VAN WIERINGEN. 1990. Nesting ecology of the Scarlet Ibis (*Eudocimus ruber*) in a small mixed-species colony of ciconiiform birds in the Venezuelan llanos. Pp. 16-27 in *The Scarlet Ibis (Eudocimus ruber): status, conservation and recent research* (P. C. Frederick, L. G. Morales, A. L. Spaans, and C. S. Luthin, eds). International Waterfowl and Wetlands Research Bureau, Slimbridge, England.
- FFRENCH, R. P. AND F. HAVERSCHMIDT. 1970. The Scarlet Ibis in Surinam and Trinidad. *Living Bird* 9:147-165.
- FREDERICK, P. C. 1987. Extrapair copulations in the mating system of the White Ibis (*Eudocimus albus*). *Behaviour* 100:170-201.
- GOCHFELD, M. 1973. Observations on new or unusual birds from Trinidad, West Indies, and comments on the genus *Plegadis* in Venezuela. *Condor* 75:474-478.
- HISLOP, G. AND C. JAMES. 1990. Status and conservation of the Scarlet Ibis in Trinidad and Tobago. Pp. 115-123 in *The Scarlet Ibis (Eudocimus ruber): status, conservation and recent research.* (P. C. Frederick, L. G. Morales, A. L. Spaans, and C. S. Luthin, eds). International Waterfowl and Wetlands Research Bureau, Slimbridge, England.
- JAMES, F. C. AND C. E. MCCULLOCH. 1985. Data analysis and the design of experiments in ornithology. Pp. 1-63 in *Current ornithology 2* (R. F. Johnston, ed.). Plenum Press, New York, New York.
- KUSHLAN, J. A. 1977a. Population energetics of the American White Ibis. *Auk* 94:114-122.
- . 1977b. Sexual dimorphism in the White Ibis. *Wilson Bull.* 89:92-98.
- . 1978. Feeding ecology of wading birds. Pp. 249-297 in *Wading birds* (A. Sprunt IV, J. C. Ogden, and S. Winkler, eds). National Audubon Soc. Res. Rept. No. 7. National Audubon Society, New York, New York.
- AND M. S. KUSHLAN. 1975. Food of the White Ibis in southern Florida. *Fla. Field Nat.* 3:31-38.
- , G. MORALES, AND P. C. FROHRING. 1985. Foraging niche relations of wading birds in tropical wet savannas. *Ornithol. Monogr.* 36:663-682.
- LUTHIN, C. S. 1983. Breeding ecology of Neotropical ibises in Venezuela and comments on captive propagation. Proceedings Jean DeLacour/IFCB Symposium on Breeding Birds in Captivity. International Foundation for the Conservation of Birds, Hollywood, California.
- MEYER DE SCHAUNSEE, R. AND W. H. PHELPS, JR. 1978. *A guide to the birds of Venezuela.* Princeton Univ. Press, Princeton, New Jersey.
- MORALES, G. 1990. Conservación de las aves zancudas en los llanos de Venezuela. Pp. 77-84 in *The Scarlet Ibis (Eudocimus ruber): status, conservation and recent research*

- (P. C. Frederick, L. G. Morales, A. L. Spaans, and C. S. Luthin, eds.). International Waterfowl and Wetlands Research Bureau, Slimbridge, England.
- AND J. PACHECO. 1986. Effects of diking a Venezuelan savanna on avian habitat, species diversity, energy flow, and mineral flow through wading birds. *Col. Waterbirds* 9:236–242.
- OGDEN, J. C. AND B. T. THOMAS. 1985. A colonial wading bird survey in the central llanos of Venezuela. *Col. Waterbirds* 8:23–31.
- PETIT, D. R. AND K. L. BILDSTEIN. 1987. Effect of group size and location within the group on the foraging behavior of White Ibises. *Condor* 89:602–609.
- RAMO, C. AND B. BUSTO. 1985. Comportamiento reproductivo del corocoro (*Eudocimus ruber*) en los llanos de Venezuela. *Memoria de la Sociedad Ciencias Naturales la Salle* 123:77–113.
- AND —. 1987. Hybridization between the Scarlet Ibis (*Eudocimus ruber*) and the White Ibis (*Eudocimus albus*) in Venezuela. *Col. Waterbirds* 10:111–114.
- AND —. 1988. Status of the nesting population of the Scarlet Ibis (*Eudocimus ruber*) in Venezuela. *Colonial Waterbirds* 11:311–314.
- RUDEGEAIR, T. J., JR. 1975. Reproductive behavior and ecology of the White Ibis (*Eudocimus albus*). Unpubl. Ph.D. diss., Univ. of Florida, Gainesville, Florida.
- SARMIENTO, G. 1984. The ecology of Neotropical savannas. Harvard Univ. Press, Cambridge, Massachusetts.
- SAS, INC. 1985. SAS user's guide: statistics, version 5. SAS Institute, Inc., Cary, North Carolina.
- SPAANS, A. L. 1975. On the present status of the Scarlet ibis *Eudocimus ruber* along the northeastern coast of South America. *Biol. Conserv.* 7:245–253.
- . 1990. Problems in assessing trends in breeding populations of Scarlet Ibises and other ciconiiform birds. Pp. 1–8 in *The Scarlet Ibis (Eudocimus ruber): status, conservation and recent research* (P. C. Frederick, L. G. Morales, A. L. Spaans, and C. S. Luthin, eds.). International Waterfowl and Wetlands Research Bureau, Slimbridge, England.
- THOMAS, B. T. 1979. The birds of a ranch in the Venezuelan llanos. Pp. 213–232 in *Vertebrate ecology in the northern Neotropics* (J. F. Eisenberg, ed.). Smithsonian Institution Press, Washington, D.C.
- AND S. D. STRAHL. 1990. Nesting behavior of Sunbitterns (*Eurypyga helias*) in Venezuela. *Condor* 92:576–581.
- VAN WIERINGEN, M. AND K. BROUWER. 1990. Morphology and ecology of Scarlet (*Eudocimus ruber*) and White Ibis (*E. albus*): a comparative review. Pp. 7–15 in *The Scarlet Ibis (Eudocimus ruber): status, conservation and recent research* (P. C. Frederick, L. G. Morales, A. L. Spaans, and C. S. Luthin, eds.). International Waterfowl and Wetlands Research Bureau, Slimbridge, England.
- WOOD, C. 1923. The Cayenne or River Ibis in British Guiana. *Condor* 25:199–201.

COLOR PLATE

The frontispiece painting by Douglas Pratt has been made possible by an endowment established by George Miksch Sutton.